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OBSERVATIONS ON THE MORPHOLOGY OF THE AROIDS

JAMES ELLIS GOW

(WITH FORTY-SEVEN FIGURES)

The material for the following observations was collected in the greenhouses of the New York Botanical Gardens, Bronx Park, New York, and was worked up by the writer during the years 1911 and 1912. The usual methods were used, the sections being cut in paraffin, and stained usually by the iron-alum-hematoxylin process, or triple stained with Delafield's hematoxylin, safranin, and orange G. The species are given in the order studied:

1. Aglaonema commutatum

At the time this work was begun, the writer was not aware of the work done by CAMPBELL on this species.[1] The results confirm CAMPBELL'S conclusions as to the seven antipodals (fig. 1) and the spherical proembryo (fig. 2). In the specimen here figured, two of the antipodals appear in process of disintegration.

2. Aglaonema nitidum

The staminate flower consists of a synandrium, cleft into lobes by 2–5 shallow creases, each lobe containing a single loculus. The youngest material examined showed the tapetum largely broken down, the pollen grains fully formed, and the first nuclear division completed. The division of the generative nucleus had not taken place. It probably occurs in the tube, and not in the pollen grain.

The pistillate flower consists of a single carpel which contains one basally attached anatropous ovule. The inner integuments are massive, the outer being thinner and never closing over the inner. In the mature embryo sac there are 10 cells, 5 of which occupy the position of antipodals, the other 5 performing the usual functions. The divisions of the endosperm nucleus give rise to a quantity of heavy-walled endosperm (fig. 3). The antipodals, or some of them, frequently persist until the sac is quite filled with endosperm. The embryo develops simultaneously with the endosperm, and is at first of the spherical form which appears to be characteristic of this family (fig. 4).

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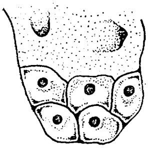
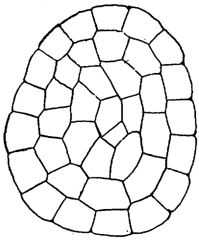
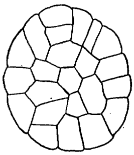
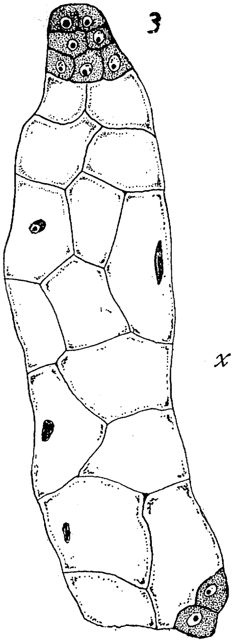
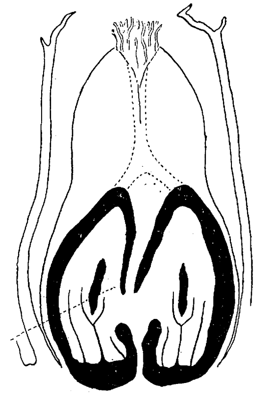
[1] CAMPBELL, D. H., Studies on the Araceae. Ann. Botany **14**:1–25. *pls. 1–3.* 1900.

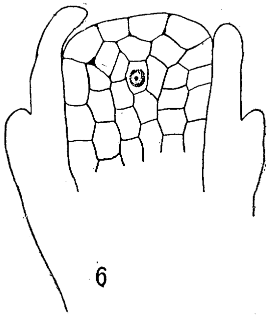












FIGS. 1, 2.—*Aglaonema commutatum:* fig. 1, seven antipodals, two disintegrating; fig. 2, spherical proembryo.

FIGS. 3, 4.—*Aglaonema nitidum:* fig. 3, endosperm; fig. 4, proembryo.

FIGS. 5, 6.—*Anthurium crystallinum:* fig. 5, longitudinal section of ovary, showing two of the six ovules; fig. 6, primary archesporial cell.

3. Anthurium crystallinum

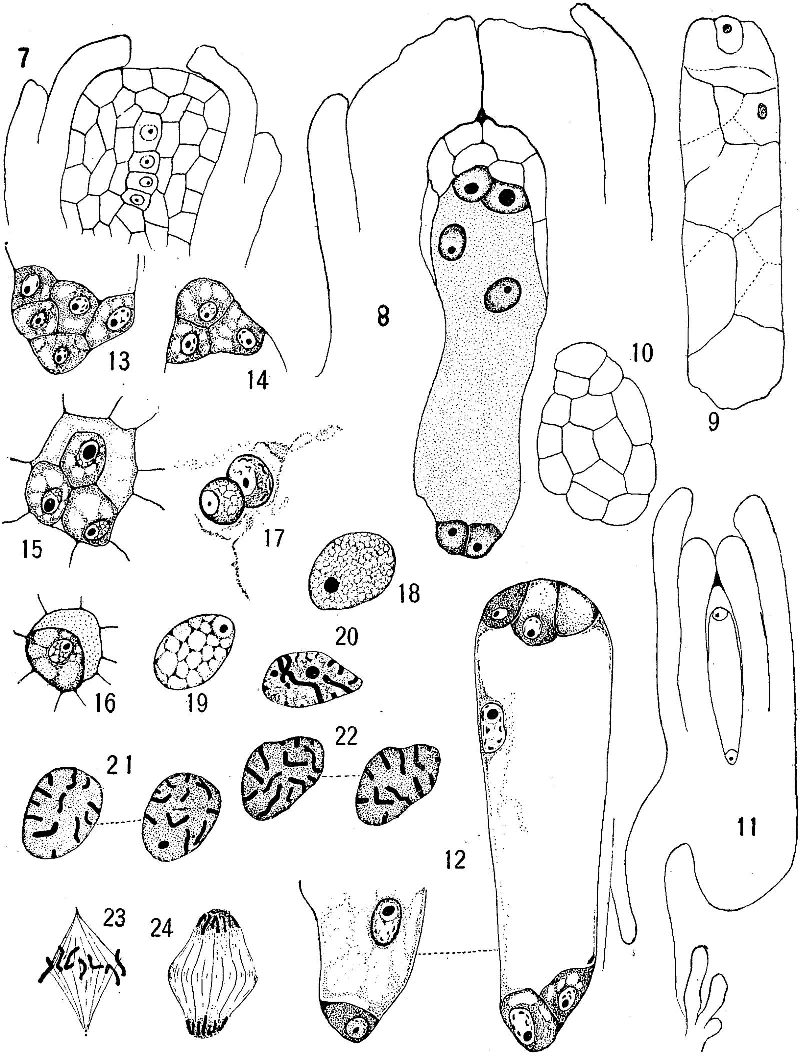
The flowers are perfect, the number of stamens varying from 4 to 6. There is a broad connective, and complete differentiation of filament and anther, in which respect the plant differs from such forms as *Arisaema* and *Aglaonema.* The appearance of the tetrads indicates that the divisions are simultaneous. The separation of the two male nuclei follows immediately on the liberation of the pollen grain in the loculus.

The compound ovary consists sometimes of two but usually of three closely united carpels, with a single truncate style whose canal is filled with viscid conducting tissue. Each of the three carpellary cavities contains two laterally attached anatropous ovules (fig. 5). The immature ovules are at first erect, but soon become reversed through the non-development of their lower surfaces. Simultaneously with their reversal, the primary archesporial cell becomes differentiated, and can readily be detected by its heavy chromatin network and ready reaction to hematoxylin stain (fig. 6). Two divisions occur, giving rise directly to 4 megaspores (fig. 7), the lower 3 of which are suppressed and break down. The functioning megaspore increases rapidly in size. The nuclear divisions are of the usual type, resulting in the formation of 8 cells. Egg, synergids, and antipodals are well marked by their positions (fig. 8). After fertilization the endosperm develops rapidly, and soon fills the embryo sac with a mass of firm, heavy-walled tissue (fig. 9), after which the division of the fertilized egg produces the usual form of proembryo (fig. 10). The ultimate fate of the endosperm in this species is not known.

4. Philodendron Wendlandii

The staminate flowers crowd the upper part of the slender spadix and consist each of a single, 4-loculate stamen without floral envelopes. Dehiscence is along longitudinal grooves. The divisions of the mother cells are simultaneous, producing the usual type of tetrad. The tapetum is rather thin (3–4 layers of cells) and breaks down early, the nuclei sometimes floating free for a time before complete disintegration takes place.

Nine carpels are arranged radially around a common axis, forming a single compound pistil. Each carpel contains two slender pseudo-anatropous ovules. It is probably correct in this case to regard the placenta as the suppressed floral axis and the ovules as lateral shoots (fig. 11). The thin integuments project far over the tip of the nucellus, the lateral portion of which becomes sup-



FIGS. 7–10.—*Anthurium crystallinum:* fig. 7, four megaspores, the uppermost one of which functions; fig. 8, embryo sac, showing six of the eight cells; fig. 9, embryo sac filled with endosperm, the latter partially diagrammatic; fig. 10, egg-shaped proembryo.

FIGS. 11, 12.—*Philodendron Wendlandii:* fig. 11, ovule of peculiar reversed type found in this and a few other species; fig. 12, embryo sac with contents.

FIGS. 13–24.—*Xanthosoma* sp.: fig. 13, the 5 antipodals; fig. 14, egg apparatus; fig. 15, same in diagonal section of embryo sac; fig. 16, transverse section showing egg; fig. 17, polar nuclei about to fuse; fig. 18, nucleus of somatic cell in early prophase; figs. 19, 20, later prophases: figs. 21, 22, nuclei showing 16 chromosomes; figs. 23, 24, spindle.

pressed through the pressure of the growing embryo sac. The latter is 8-celled, the arrangement being of the usual type (fig. 12).

The endosperm is heavy-walled as in *Anthurium*, and the proembryo is egg-shaped.

5. Philodendron gloriosum

The ovule is much like that of the species just described. Like it the embryo sac is 8-celled, the endosperm is heavy-walled, and the embryo spherical to ovate.

6. Arum maculatum

This plant was obtained from a local florist and grown in pots. Owing to difficulty in the fixation of material the earlier phases cannot be given. It has the usual 8-celled embryo sac and spherical proembryo, and a thin-walled endosperm which is persistent in the seed.

7. Xanthosoma sp.

Through accident the label attached to this specimen was lost in transit. As the material was cut into cubes and in the fixing medium its identity could not be traced.

Each cell of the tricarpellate ovary contains two slender anatropous ovules. A series of long conducting cells lines the interior of each carpel and extends to the micropylar extremity of the ovule. The extremity of the truncate style is covered with glandular papillae. The ovule is extremely slender, as in *Philodendron*, but is sessile and does not occupy the reversed position. There appear to be 5 antipodals (fig. 13), the other contents of the embryo sac being what might be anticipated in any angiosperm (figs. 14–17).

Many of the cells surrounding the embryo sac were found to be in an active state of division, probably owing to the increase necessitated in the accessory tissue by the enlargement of the embryo sac. This gave a good opportunity to study the phases of homotypic division. No continuous spirem stage could be discovered. The chromatin reticulum is at first very fine, the strands later shortening and thickening, and finally breaking into an irregular mass of coarse threads which soon resolve themselves definitely into 16 chromosomes. Early splitting of the chromosomes was noticed in a few cases (figs. 18–24).

Homalomena argentea

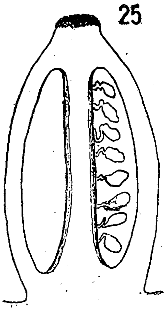
The lower part of the cylindrical spadix is crowded with the pistils, interspersed with numerous staminodia; the upper is crowded by the equally numerous stamens. Each pistillate flower consists of a single ovary, which in turn is made up of 3 foliaceous carpels. The ovules spring from the infolded edges of the placentae, and are arranged in 6 ranks (fig. 26). There is no open stylar canal, but the inner tissues of the style are loose and spongy (fig. 25). The anatropous ovule is mounted on a slender funiculus. When it has fully developed, the inner integument is massive and closes over the tip of the nucellus (fig. 28). The outer remains as shown in the figure.

The primary archesporial cell is somewhat larger than the surrounding cells (fig. 27). It divides once transversely, and of the two resultant cells the outer one functions, the inner one being broken down and absorbed. Whether the latter is to be regarded as one of a "row of two" or as a vestigial tapetum is purely an academic question. Functionally it is a tapetal cell. The embryo sac contents consist of the usual 8 cells arranged in the typical manner (fig. 28).

9. Stenospermation popayanense

A curious anomalous form was found in the Botanical Gardens under the name *Stenospermation pompayanense*. This may be a monstrosity, but of such a sort that its description should be of interest, and may have some morphological significance. Only one plant was found, and it bore no staminate flowers, and apparently no normal stamens, although *Stenospermation* is described by SCHOTT as having hermaphrodite flowers, with "stamina quattuor, singulo pistillo annexa." It may be, therefore, that this is not a member of the genus *Stenospermation*, although so labeled. The specific name *pompayanense* is an old synonym of the original name *popayanense*.

In the form under discussion, whatever its real identity, the long slender spadix is covered with lozenge-shaped blossoms which remind one at first glance of the closed blossoms of *Symplocarpus foetidus*. The resemblance is purely superficial. In *Symplocarpus*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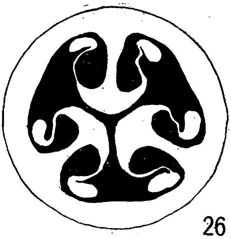
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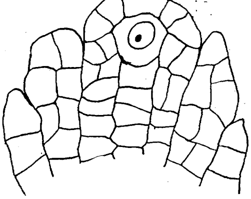
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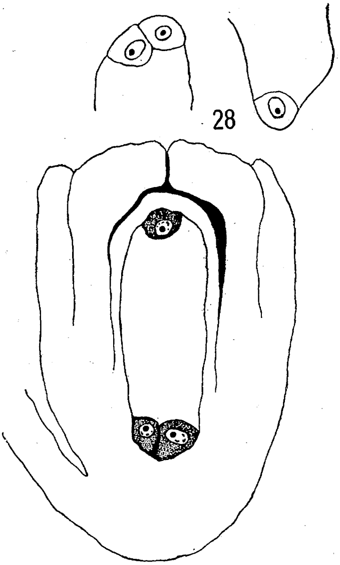
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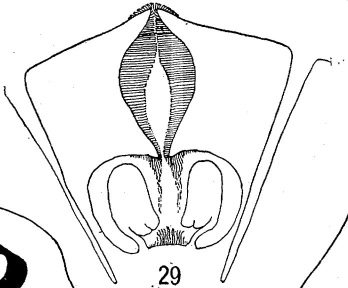
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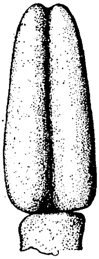
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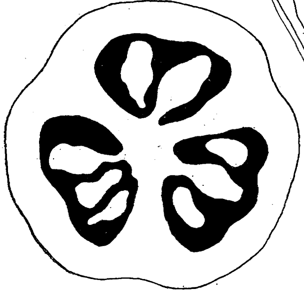
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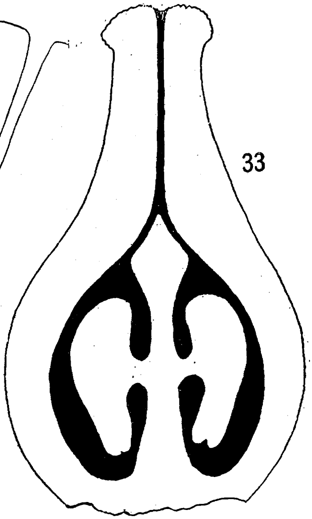
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FIGS. 25–28.—*Homalomena argentea:* fig. 25, longitudinal section of ovary; fig. 26, transverse section of ovary; fig. 27, primary archesporial cell; fig. 28, embryo sac with six of the eight cells.

FIGS. 29–31.—*Stenospermation popayanense* (?): fig. 29, vertical section of carpel, showing ovules in position, and the stylar canal filled with conducting cells; fig 30, stamen in cavity of pistil; fig. 31, pollen grain.

FIGS. 32, 33.—*Richardia africana:* fig. 32, transverse section of ovary, showing position of ovules; fig. 33, longitudinal section cutting two ovules.

the lozenge is formed by the infolded edges of the floral envelopes, while the central projecting "button" is produced by the protrusion of the anther tips. In the so-called *Stenospermation* the lozenge is merely the smooth upper surface of the thick-walled carpel, and there are no floral envelopes and no stamens surrounding the carpel. The "button" is the projecting stigmatic area (fig. 29). In the cavity of the carpel are found a circle of 4–8 erect anatropous ovules. Owing to the hardening of the gum contained in the tissues of this plant (and which resisted all reagents), sections could not be cut in paraffin, and the internal structure of the ovule cannot be described. Rather thick sections of the carpel were cut in celloidin, showing details of the stylar canal, and the curious crowded conducting cells as figured.

While all the blossoms are alike so far as outward appearance is concerned, a certain number of them (about 40–50 per cent) are found to bear stamens in place of the ovules just described. They are arranged in a circle, similar to the arrangement of the ovules, have large, well developed anthers with a broad connective, and when examined appeared about ready for dehiscence. The filaments of course are extremely short. If they lengthen later, no suggestion of such lengthening appeared in the material under examination. The exterior appearance of the "ovary," if such it may be called, is exactly the same whether it contains ovules or stamens. When torn open and mounted in glycerin, the anthers were seen to be filled with matured and normally formed pollen grains. No extra-carpellary stamens were found. The staminate carpels (if such they may be called) were found mixed among the pistillate, but somewhat more numerous toward the upper end of the spadix. In a very few cases the same carpel was found to house both stamens and ovules.

10. Arisaema triphyllum

The embryogeny of this species has been already discussed.[2] For the investigation of the microsporangium bulbs were collected in September and the blossoms dissected out. It was found that the entire microsporangial structure was fully matured at that time; the mother cells had disappeared and the pollen grains were found lying free in the loculi of the anther. Almost all the bulbs were such as had borne pistillate blossoms the preceding season; in fact the material was collected after the early frosts and was discovered by means of the conspicuous clusters of bright red berries after the withering of the leaves. A very few of the bulbs were laterals formed from the central bulb during the growing season. Two or three of the bulbs collected contained a monoecious spadix. Two-thirds of the balance contained staminate blossoms only. *Arisaema* seldom bears staminate and pistillate flowers on the same spadix, but the indication is that the plant that bears pistillate flowers one year bears staminate flowers the next. It is, in a way, consecutively monoecious, seldom simultaneously monoecious.

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[2] GOW, JAMES ELLIS, Embryogeny of *Arisaema triphyllum*. BOT. GAZ. **45**:38–44. *figs. 24.* 1908; also MOTTIER, DAVID M., On the development of the embryo sac of *Arisaema triphyllum*. BOT. GAZ. **17**:258–260. *pl. 18.* 1892.

The loculi of the stamens contained many normal pollen grains, but far more small suppressed grains, the ratio being about 2:1, suggesting the inability of the plant to muster sufficient energy to mature all the pollen it produces.

11. Richardia africana

This plant, the *Calla aethiopica* of the florists, was found in every stage of development at the Cedar Rapids greenhouses, and fixation proved extremely easy owing to the absence of mucilage in the tissues.

The upper portion of the slender spadix is covered by a densely crowded mass of stamens, while the pistillate flowers occur below. SCHOTT describes the pistils as "organis neutris tribus cincti," but in perhaps a fourth of the blossoms these "neutral organs" turn out to be functioning stamens, while in the remainder they are staminodia, or staminal rudiments.

The cylindrical ovary consists of 2, 3, or 4 carpels, the anatropous ovules being borne on the central placenta, which here represents the united carpellary walls. Two to four ovules occur in each carpellary cavity (fig. 32), and a separate branch of the open stylar canal runs to each cavity. The ovule is anatropous, and of foliar origin, since it springs from the carpellary wall. The funiculus is laterally attached. There are the usual two integuments, which grow well out beyond the tip of the nucellus (fig. 33). The ovule first appears as a lateral projection nearly filling the cavity of the immature carpel. As the latter enlarges, the ovule keeps pace with it. The integuments begin to appear before it assumes the anatropous position (fig. 34). The primary archesporial cell is differentiated about simultaneously with the appearance of the integument, and even in its resting condition may be recognized by its greater size (fig. 35). After, or simultaneously with, its differentiation, the tip cells of the nucellus divide by periclinal walls, forming two cell layers outside the archesporium. No primary parietal cell is formed. The primary archesporial cell is in this species the spore mother cell, and develops directly into an embryo sac without the previous formation of a row of megaspores. The first division occurs early (fig. 36). The later divisions follow in the usual order (figs. 37–39), and before their completion the integuments have reached complete maturity, closing over the tip of the nucellus.

The account just given represents the normal development of the ovule and embryo sac in *Richardia* and holds true in perhaps 5 per cent of the plants examined. In most cases, however, the plants not only fail to set their seed, but will not do so even when artificially pollinated. I refer here solely to the plant as I have observed it growing in local greenhouses, and to the individuals (some 150) on which I have tried the experiment of artificial pollination. The observation of gardeners, so far as they have been consulted, confirms the conclusion that the vast majority of plants of the strains here cultivated, and under the conditions existing in local greenhouses and gardens, cannot be made to produce seed. BURBANK, on the other hand, reports that the *Richardia* as it grows wild in California matures seed in great abundance.[3]

The behavior of the artificially pollinated ovaries is peculiar. Ovaries not artificially pollinated shrivel in 10–15 days after reaching maturity. Pollinated ovaries behave otherwise. A large

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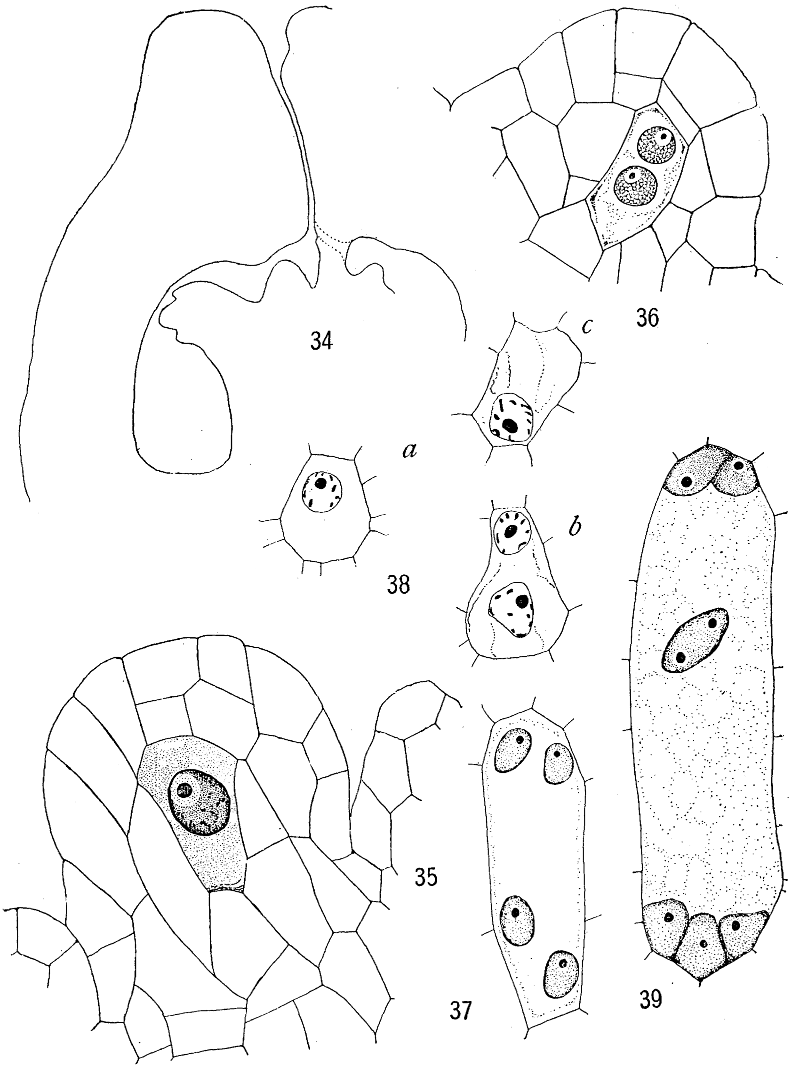
[3] "The calla lily, in all its varieties, blooms and seeds in the utmost profusion here in California, setting big plump seeds in abundance. This includes all the yellow, white, and black varieties. I think the cause of not setting seeds in the east is wholly climatic."—From a private letter addressed to the writer.



FIGS. 34–39.—*Richardia africana:* fig. 34, immature carpel, containing developing ovule which is just beginning to show the anatropous character; fig. 35, primary archesporial cell; fig. 36, first nuclear division in formation of embryo sac; fig. 37, four-nucleate embryo sac; figs. 38, 39, mature embryo sac.

number of flowers were pollinated early in January. Three weeks later the ovaries had swollen to the size of large peas, and the gardener—a veteran in the growing of the *Richardia*—was confident that seed would be set. Within the following week most of these had begun to wilt, but a very few continued to grow until they were as large as small hazel nuts. Within two weeks almost all were withering, and from then on the molds rapidly made away with them. Five per cent or less of the pollinated plants produced seed.

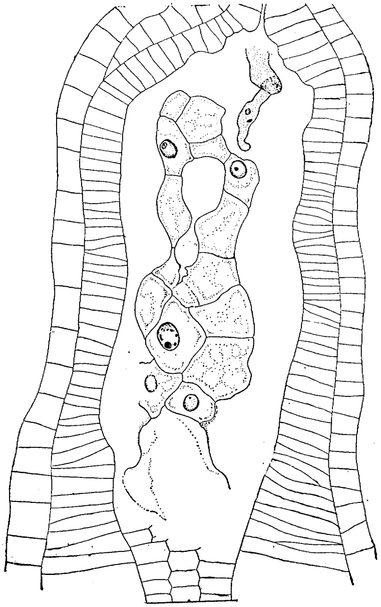


FIG. 40.—*Richardia africana:* disintegrating sterile nucellus and tip of pollen tube.

The explanation of this behavior is to be found in the fact that the greater number of ovules are congenitally sterile and develop no embryo sac. In some cases no cell can be discovered that can be definitely identified as a primary archesporial cell. In other cases it would seem that a potential archesporial cell makes its appearance, but fails to complete its normal course of development. The latter is to be inferred from the fact that the number of primary archesporial cells encountered in the very young material vastly exceeds the number of embryo sacs in the more mature material.

Sections of pollinated pistils containing sterile ovules demonstrated the fact that, in some cases at least, the pollen tube penetrates a sterile ovule, and reaches the tip of the nucellus. The fact that the pollinated sterile ovaries reach a considerably higher stage of development before withering than do unpollinated ovaries of the same sort would appear to be due to the stimulus of pollination. At all events, the writer can find no other cause to which it can reasonably be attributed. The direction of the pollen tube into the ovule is probably determined by the presence of nutritive material in that quarter, since the nucellar cells, and even the tip cells of the integuments often become somewhat swollen and glandular and break down readily. If this be the case, the tube should enter a sterile ovule quite as readily as a fertile one. In a number of cases remains of shrunken pollen tubes were observed near or in contact with sterile nucelli (fig. 40).

The sterile nucellus finally breaks down, the process usually beginning within, and sometimes resulting in, the formation of an interior cavity before the disintegration of the outer cells (figs. 40, 41), and the nuclei of the cells occasionally lie free in this cavity before disintegration. The breaking down of the nucellus finally leaves the cavity within the integuments completely empty; the ovule soon collapses and begins to decay.

In the case of fertile ovules, the embryo sac is of the usual 8-celled type. The cavity soon becomes filled with a mass of thick-walled endosperm cells, and the endosperm is persistent in the seed. The proembryo develops a little later than the endosperm, and is spherical in shape, finally lengthening out and developing a distinct notch (fig. 42).

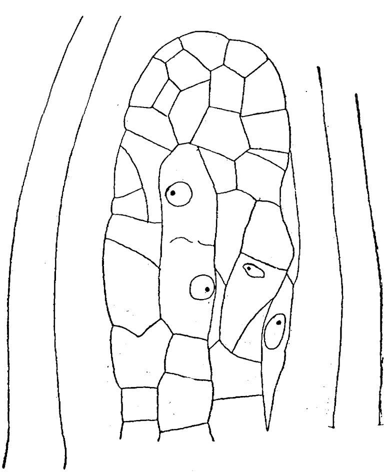
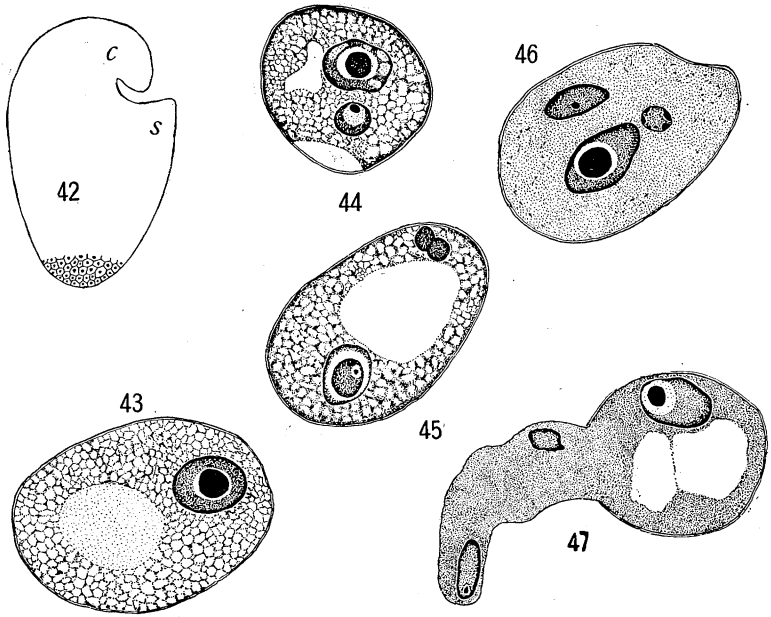


FIG. 41.—*Richardia africana:* sterile nucellus; disintegration just beginning.

Anthers dissected out, before the appearance of the flower bud as a swelling under the leaf-sheath, disclosed many large multinucleate mother cells. Tetrads are formed by successive divisions, the 4 daughter cells lying in the same plane. Material taken from a plant in which the flower bud was beginning to form a prominent swelling within the stem disclosed mature pollen grains filling the loculus of the anther. The latter has the usual thickened epidermal layer of rather small cells, inside which is an endothecium of large cylindrical cells with riblike thickenings. The tapetum consists of a layer 3 cells deep and disintegrates early. The spores lie in a mass of gelatinous material, the remains of the former tapetum, and scattered among them are many small, ill developed cells which show a tendency to break down. These are abortive pollen grains, or possibly in some cases abortive mother cells.



FIGS. 42–47.—*Richardia africana:* fig. 42, embryo in early stage of development; *c*, cotyledon; *s*, stem tip; fig. 43, mature pollen grain previous to nuclear divisions; fig. 44, pollen grain previous to division of generative cell; fig. 45, male cells in contact; fig. 46, tube nucleus and male cells, the latter abnormal as to shape and comparative size; fig. 47, sprouting pollen grain.

There is a great lack of uniformity in the divisions within the pollen grain. In one case (fig. 43) all were delayed until after dehiscence; but this is certainly very unusual. The first nuclear division, by which the generative nucleus is differentiated, usually occurs early. The generative nucleus does not surround itself with cytoplasm and a distinct cell membrane, but retains its nuclear character after division. Usually it divides before dehiscence occurs (fig. 45), although a number of grains were taken from dehiscing anthers in which it was found that this division had not yet taken place. Grains were sprouted in weak solutions of glucose and lactose, and examined unstained, or stained in a weak aqueous solution of hematoxylin. One of these is indicated in fig. 47.

Summary

1. The development of the archesporium in aroids follows no uniform rule. In one species studied,[4] the primary archesporial cell produces two megaspores, the outer one of which functions; in two cases there are four megaspores, the outermost one of which functions; in one case the primary cell produces two cells, one of which may be a tapetal cell; one species develops four megaspores in the same horizontal plane, and the functioning one then develops a tapetal cell at its upper end; one species develops four megaspores, the innermost of which functions; and in one case the primary sporogenous cell develops directly into an embryo sac.

2. The number of antipodals varies from 3 to 11, four species having regularly more than 3. This is a relatively primitive feature, and occurs in other primitive orders.

3. Previous to the work here reported, embryos of the spherical type lacking a suspensor had been reported by CAMPBELL in *Pistia*, *Dieffenbachia*, and *Lysichiton*. The writer has confirmed CAMPBELL'S observation with regard to *Dieffenbachia*, and has discovered the same sort of embryo in *Nephthytis*, *Philodendron*. *Arum*, *Aglaonema*, *Anthurium*, *Arisaema*, *Symplocarpus*, and *Richardia*. It seems clear that this type of embryo is characteristic of this family.

4. *Richardia* as here cultivated in the greenhouse has usually a sterile nucellus and does not develop an embryo sac. The disintegrating nucellar cells act as conducting tissue, and the pollen tube enters sterile nucelli, although gametic attraction cannot exist. The direction of the tube is conditioned on the presence of nutritive material.

5. Reduction of parts is indicated by the presence of staminodia in several of the species studied.

6. In an abnormal specimen supposed to belong to the genus

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[4] GOW, JAMES ELLIS, Studies in Araceae. BOT. GAZ. **46**:35–42. *pls. 4–6.* 1908.

Stenospermation functioning stamens replace the ovules in many of the carpellary chambers. This reminds one of a somewhat similar abnormality noted by CHAMBERLAIN in *Salix*, and of characteristics noted by TREUB in *Balanophora* and *Loranthus*.

7. In three species investigated with regard to number of chromosomes the homotypic number was found to be 16.

8. Tetrad formation in the anthers of some species is by means of simultaneous, in others by successive, divisions.

9. In *Richardia* the male nuclei are not surrounded by a definite cytoplasmic envelope, and the division producing them is often delayed until dehiscence or later. Sometimes the earlier divisions are similarly delayed.

10. The bulb of *Arisaema* may bear staminate and pistillate blossoms in alternate years.

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